MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 14, NUMBER 3 JULY, 1957

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PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

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Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price $4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

CALIFORNIA BOTANICAL SOCIETY, INC.

THE CONCEPT OF THE FLOWER AND THE THEORY OF HOMOLOGY[1]

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In seeking sound concepts around which to build our ideas of the taxonomy of the flowering plants, we find that confidence in our concepts of the flower has steadily deteriorated since the exposition and later clarification of the classical theory of the flower and especially since the publication by Zimmermann (1930) of the telome theory. The ideas embodied in the classical theory—namely, that the parts of the flower are metamorphosed leaves—had their beginnings early in botanical history, going back at least to Linnaeus and several of his associates. The most significant enunciations of the theory, however, are accorded to Caspar Friedrick Wulff (Samassa, 1896) and to the poet-philosopher Wolfgang von Goethe (1790). It is important to realize that the classical theory embodied the concept of homology that was being discussed by the 18th and 19th century anatomical philosophers of Germany and France, including also such men as Cuvier (1800), Oken (1807), and St. Hilaire (1807). The concept originated in the thinking of the classical geometricians and was here being applied to biology. The language was vague because its abstractions, although clear to its authors, were burdened with confusions of logical types that led to confusion of understanding among the readers in their attempts to apply it. For instance, Goethe spoke of the parts of the flower as being "metamorphosed leaves" while Oken created bewilderment among zoologists by speaking of the "humerus of the head." These ideas became variously known in botany as the "classical theory of the flower" or, more broadly, as "the theory of morphology," alluding here to the concept of homology that was embodied in it. It met with immediate criticism as presenting an illogical consequence, since "that which never was a leaf could scarcely be a metamorphosed leaf."

There followed a period of great discussion. Of the clarifications which emerged, that expressed by the British botanist, Lindley (1838, p. 59), seems especially worthy of our attention because it constitutes one of the first clear expressions of the concept of morphological equivalence. Said

[1] The substance of this paper was presented to the Eighth International Botanical Congress in Paris in 1954 under the title, "The Controversy of the Flower and its Bearing on Phylogenetic Taxonomy." Prior to this it was presented in seminars at the Davis and Berkeley campuses of the University of California and at Stanford University. Since these preliminary presentations the manuscript has been amended to indicate the formal nature of the Theory of Homology, and the title has been changed to indicate more precisely the scope of the paper.

Acknowledgments are due to Jean Langenheim for many lively discussions leading to the organization and clarification of the subject matter, and to Annetta Carter, Francia Chisaki, Helen Sharsmith, and Isabelle Tavares for assistance in perfection of the manuscript.

MADROÑO, Vol. 14, No. 3, pp. 81–112, July 30, 1957.

Lindley, "It has been observed in a report made to the British Association at their meeting in Cambridge in 1833, when adverting to this doctrine, that when those who first seized upon the important but neglected facts out of which the modern theory of morphology has been constructed, asserted that all appendages of the axis of the plant are metamorphosed leaves, more was certainly stated than evidence would justify: for we cannot say that an organ is a metamorphosed leaf which in point of fact, never was a leaf. What was meant, and that which is supported by the most conclusive evidence, is, that every appendage of the axis, whether leaf, bract, sepal, petal, stamen or carpel, is originally constructed of the same elements, arranged upon a common plan, and varying in their manner of development, not on account of any original difference of structure, but on account of special and local predisposing causes; of this the leaf is taken as the type because it is the organ which is most usually the result of the development of those elements; is that to which other organs generally revert when, from any accidental disturbing cause, they do not assume the appearance to which they were originally predisposed; and moreover is that in which we have the most complete state of organization."

There are several interesting ideas embodied in Lindley's statement with which we may or may not agree. But what is important to my thesis is the concept of morphological equivalence which assumes that equivalent structures have had a like origin, are arranged in accordance with a common plan, and differ from one another in their further development as a consequence of special and local predisposing causes. This assumes some sort of identity in the early ontogenetic stages. Some such ideas as here expressed have governed the thinking in morphological research for a century and a half. To a large measure they have been responsible for the common practice of interpreting one structure in terms of another on the assumption that all structures are deviations from a prior "common plan." Each structure is assumed to have arisen through the ontogenetic modification of a pre-existing structure. Thus the concepts of the classical theory and of morphological equivalence, at least as to their explanation, are definitely ontogenetic concepts whose explanation rests in knowledge of ontogeny.

The alternative to these ideas is that structures arise anew, possibly upon a foundation of the old, but in no sense to be regarded as being a modification of the old. A structure arising in this manner is said to arise *sui generis*. This idea also has followers, among them Gregoire (1938). I do not imply in placing this theory in apposition to the preceding that it does not also entail an ontogenetic explanation.

As we look into modern concepts of the flower we find that both the classical theory and the concept of homology generally are being seriously questioned as logical bases for morphological interpretation. New approaches to the problem are being investigated outside the scope of the classical theory and the concept of homology. Since a sound taxonomy of

the flowering plants and especially a sound basis for phylogenetic interpretation must rest upon an understanding of the flower, I have attempted to review these concepts and evaluate this controversy in the hope of developing at least an adequate working hypothesis concerning the flower that might prove of value to taxonomy.

As we examine the various theories of the flower that have deviated from the classical theory, nearly all point to the fact that the classical theory fails to explain one aspect or another of the flower. Most workers pointed to various features of the carpel, especially to its relation to structures resulting in an inferior ovary, as not being interpretable in terms of the homologies of appendages. With these difficulties as a beginning, other difficulties became apparent, and there ensued a re-evaluation of all points of difference between carpels and typical leaves and of other parts of the flower in their departure from appendages homologous with leaves. Some workers have investigated the organogenesis of the flower apex in comparison with that of the shoot and have pointed to differences. As a result of their researches upon these problems, Thomas (1934), Thompson (1935), Gregoire (1938), and Lam (1948) insist that an entirely new approach to the interpretation of the flower is called for. In fact Gregoire would overthrow homology as being inapplicable to any comparison of the flower and the shoot, and would insist that the flower is an organ *sui generis* and not in any ontogenetic sense comparable with a shoot. This point is amply discussed and the argument met by Boke (1947).

I do not intend systematically to discuss here the points raised by each of these investigators; what I am concerned with is a re-evaluation of the investigative and intellectual approaches to the problem.

There are at least two basic approaches to the study of the flower. The first of these, the traditional method, employed the concept of homology as a system of logic interpreting structures in terms of abstract categorical levels of morphological equivalence, without necessarily knowing the precise details of ontogenetic elaboration beyond identity, origin, and relative position. This method has been useful, for, although it did no more than categorize structures in terms of the formal relations of a unitary classification, it aided in determining what were comparable structures and at the same time provided a basis, on the one hand, for explaining points of likeness between two structures, and, on the other, a point of departure for ordering and explaining the differences between structures. This has been the chief use to taxonomy of the classical method of morphology.

The other approach to the problem seeks more precise information. It presumes to base its interpretations upon discovering the details of ontogenetic elaboration. Obviously, if such researches are faithfully followed to their conclusion and the details of ontogenetic elaboration carefully worked out, we will have a considerable body of fact upon which to base our judgments and our interpretations, but such facts will in no way eliminate the need of a logical system nor obviate the necessity of establishing intellectual concepts for interpretation.

As we review the controversy of the flower, it appears to be a controversy between these two approaches to the interpretation of the flower. The researches of Zimmermann and his development of the telome theory call for detailed investigation of anatomical organization and ontogeny at a level of structural organization below that envisaged in the system of logic developed by Goethe for the classical theory of the flower, which operated strictly on the level of gross organography. If we are to employ the concept of homology to function at this more detailed level, we will have to redesign our system of logic so that it will be useful in terms of the structures that pertain at this level of organization. To some, the telome serves this purpose (Zimmermann, 1930). The telome is defined in terms of empirical criteria derived from the structure of the extinct Psilophytalean genus *Rhynia* wherein the terminal segment of the axis beyond the last dichotomy is accepted as the basis of the concept of the telome. The segment of the axis upon which the telome rests is called the mesome. Thus telomes, as they give rise to new telomes in their ontogeny, become mesomes. It follows that if we can get at the facts of anatomy, we should be able to trace, through the structure of the individual, the ontogenetic history of telome elaboration, and, through the ontogeny of elaboration of the individual, we may be able to interpret the phylogeny of telome differentiation in the origin of organs. This is the simple logic of the case, and we read such phrases as "seeking the evidence of ancient dichotomies" (Lam, 1948). Obviously the details of morphological differentiation in the higher plants are more complicated than those evident in the fossil *Rhynia*. These complications are systematically explained in the telome theory by a series of elementary processes accounting for the origin of the telome and its phylogenetic elaboration to produce the most complicated of higher plants. I shall not go into this in detail, but will discuss some limitations to its use in comparative morphology. It is sufficient here to call attention to the fact that, like the cell, the telome is thought of as a ubiquitous structure in the plant.

Not all of the discontent with the classical theory emanates from followers of the telome theory. My point is that the wave of reactivated discontent began with the detailed anatomical analysis of structure called into operation by the telome theory and rests primarily upon evidence pertaining to an anatomical level of organization not adequately accounted for in the classical theory of Goethe based on organography.

It should be clear that the telome theory—namely, that plant structures are compounded of telomes in accordance with the operation of the elementary processes — like the classical theory and the principle of homology is a system of logic. As a system of logic it is designed to interpret structures on the basis of criteria significant to telomes and the elementary processes significant to their elaboration. The principle of homology, on the other hand, is a system of logic designed to interpret structures through the logic of comparison resting upon comparable criteria significant to morphological equivalence. The logical consequences of the prin-

ciple of homology are not to be judged by the criteria of the telome theory. These criteria are pertinent only to the logical system for which they were developed. There is nothing inherent in the telome theory that can invalidate either the classical theory or the principle of homology. We, as the designers of these systems of logic, can, if the facts warrant, say that one system explains the situation much better than the other and we may accept or reject on that basis. On the other hand we may alter the system of logic to make it more effective, and, if the altered system proves to be more efficacious, we may replace the old with the new.

Having investigated the problem of the flower both by studying its presentation in the literature and by reviewing the structural features of a large number of different kinds of flowers, I have assessed this controversy as resting primarily in difficulties with our system of logic, in part with our failure to establish adequate diagnostic criteria for the categories into which we would classify the structures of the flower and in part with a confusion of description with ontogeny and phylogeny, rather than with any unusual difficulties inherent in floral anatomy. The chief anatomical difficulty is largely a matter of determining 'when is a structure a new structure?' meaning by this, when does it depart from being an integral part of the structure that bears it? This, I think, can be answered strictly within the framework of the principles of homology, viewing each case, to be sure, in its ontogenetic setting, but primarily viewing each structure for what it is.

In discussing the concept of homology I shall employ a diagrammatic design (fig. 1) which may be spoken of as an organization system (Woodger, 1929). This is strictly a design for displaying an idea, and as I employ it, it is not to be construed as meaningful to any other purpose. Its purpose here is to display the scope and detail of the application of the concept of homology as it appears serially in the plant, how homology is to be interpreted in cases of regeneration, and through this, how structures that may otherwise appear as anomalous may be effectively explained. From serial homology we may proceed to general homology, a transitive relation which rests upon the notion that "things equal to the same thing are equal to one another." We will, however, use the term "equivalent" in the sense we attribute to Lindley, rather than the term "equal," which implies detailed identity. I shall employ as exemplary the homologies of the appendages of the axis of the shoot and of the flower in the flowering plants.

Organization System of a Higher Plant

Whether an organism develops from a one-celled zygote, from a single meristematic cell, or from a group of meristematic cells, there is a pattern of organization resulting from its ontogeny that reflects the plasticity of the cell in its capacity for division and differentiation. This pattern of organization has a dual aspect. It is reflected first as an increase in structural complexity brought about simply by the continued increase and

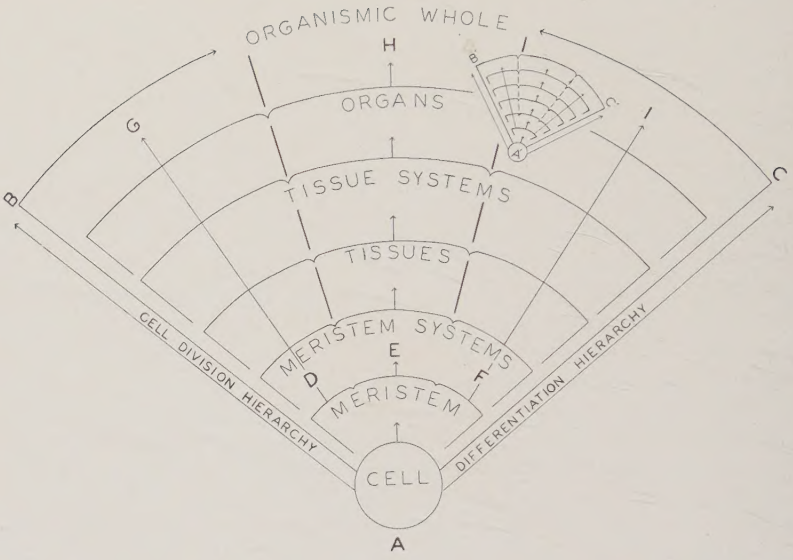

FIG. 1. Diagram of organization system resulting from increase in complexity due to cell division and cell differentiation.

A to BC represents the complexity arising purely from the multiplication of cells. The three cell lineages A to DG, A to EH, and A to FI represent differentiation through the activities within each of the three meristem systems and represent a complexity resulting from cell differentiation. Regeneration homology is indicated by A′ B′ C′ where a new system is generated at the organ level. Interpretation is achieved by correlating A′ with A, B′ with B, and C′ with C.

disposition of large numbers of cells, as A to BC (fig. 1), especially where the pattern results from different planes of cell division. The pattern of organization is reflected secondly as an orderly increase in complexity resulting from the differentiation of the meristem DEF and channelling the diversity into lineages of differing tissues, tissue systems, and organs ordered in accordance with their respective meristem origins, as A to DG, A to EH, and A to FI. Let us suppose that these represent the lineages originating in the three meristem systems from promeristem through protoderm, procambial strands, and ground meristem, and the cell and tissue lineages of each meristem system to its structural destiny. By superimposing the idea of increased structural complexity through cell division on different planes over that of the results of meristematic differentiation, as shown in the system chart (fig. 1), we obtain the impression of an organization system that may be of great utility in the interpretation of comparable structures on any given plant, as well as a basis for determining what on any given plant is comparable; through such serial comparison we may determine what structures on different plants are comparable. We may interpret the design as constituting a hierarchy of different levels of

organization in which each of the lower levels participates within the limits of its meristematic origin in the structural organization of each successively higher level, and at length each is an integral part of the organismic whole. Analytically this presents a design in order approachable through mathematical induction.

Aside from the cell division hierarchy and the resulting segregation mentioned above, it is also possible to trace in these same patterns hierarchies of structural specialization and of associated functional specialization. And since each phylogenetic step of structural advance was accomplished as a precise step in the ontogeny of an individual through the activity of mutagenic agencies or other cytological phenomena by which an individual deviated from its predecessors to the extent of this step, the hierarchy of organization also reflects, to a limited extent, through logical implication, the basis for a phylogenetic explanation as it relates to structural pattern. The reasoning here is clear, but because of the nature of the facts it may be clearer than the evidence. The reasoning is as follows. There is no step in phylogeny that structurally is not first evident as a step in the ontogeny of an individual regardless of its cause. So far as the empirical phenomena upon which these rest are concerned, and especially as phylogeny relates to any particular phylogenetic step, ontogeny and phylogeny are one. It is possible to abstract successive steps in phylogeny out of their context of successive ontogenies. We may then speak of a unitary phylogenetic sequence. Through the many changes that have involved the structural differentiation of plants, however, it is no longer possible to separate these as discrete historical steps in either phylogeny or ontogeny. Because of this, the ideally sound biogenetic law of Haeckel (1876) that ontogeny recapitulates phylogeny is difficult of application except in very general terms. The common properties of equivalent structures must be assumed to represent their common ancestral connections from which they deviate in their separate ontogenies and phylogenies. It would seem, therefore, that the concept of morphological equivalence rests, to this extent, on the biogenetic law. In our organization diagram, therefore, as they relate to an individual, the older phylogenetic facts are probably to be found lower in the system than are the younger. (In this predecessor-successor relation of morphological facts based upon levels of identity, we see the basis for the connected system necessary for the logic of homology.) To my thesis, the operation of the biogenetic law is most clear when a preceding structure serves as a structural foundation for a phylogenetically following structure and must be resynthesized in each ontogeny in order that the following structure may be synthesized. This may be the full scope of the meaningfulness of the biogenetic law in plants.

The Cell and its Role in Ontogeny

Since each individual begins as a single cell and each step in the complexity and differentiation of the whole results from cell division into like or different kinds of cells, it will be apparent that all known operational

dynamics in the structural ontogeny of the individual are on the level of dividing cells, plus any subsequent modifications of any individual cell. Dividing cells occur at nearly all structural levels of the hierarchy, and such meristematic cells, through the subsequent development of descendent cell lineages, may either carry the main organization system toward its completion or may initiate a cell lineage capable of developing a new structure that may be an ontogenetic departure from the structure in which the original cell arose. Thus at the junction of the petiole and the blade of the leaf of *Tolmiea menziesii* and in the crenations on the leaf margin of various species of *Bryophyllum*, buds develop that generate new plants as complete as those which develop from seed. Organographically these initiating meristems occur at a high level in the organization system. However, in the inception of this activity we must think of the meristems as returning to a lower level in the system and thus as regenerating a new system. It is a very important fact that neither the resulting system nor the structure produced in any way distorts the interpretation of the organ on which these initiating meristems arose. In the cases here mentioned the organs bearing the new "system" are still and always will be leaves.

How and where new anatomical lineages may develop and to what extent they develop will depend upon the "special and local predisposing causes of ontogeny." These predisposing causes may result in the production of such structures as a sporangium on a sporophyll, the extension of a structure by toral growth, the production of some teratological structure, the development of a tissue, or the extension of a vascular system. If such a structure is defined in terms of its inherent properties, it is primarily significant for what it is. Only if it is defined in terms of some positional relation is it ever significant for where it is. In some cases it may be significant to the defining type of the structure that bears it, as for instance, a megasporangium on a sporophyll is significant to this sporophyll being also a carpel; but neither what the sporangium is, nor where it is, is in any way significant to the interpretation of the carpel as being also an appendage.

Such ontogenetic and phylogenetic facts are useful in the explanations of likenesses and differences by which we classify, but they neither serve to describe nor define the classes of like structures. As we contemplate these matters we are first concerned with the identity of the structure, then with its connected relations in a classified system of structures. We discover in the properties of our material the order and connectedness that relates the classes of structures. We then explain it with our notions of ontogeny and phylogeny. Our first task is to discover and describe and thus determine what are homologous structures. We move then to explanation.

It would seem important, therefore, that if we are to seek to explain such structures and their relations, we must direct our attention first to the organization level of dividing and differentiating cells regardless of the higher organization level of which these cells may have been a part.

The primary fact is the capacity of a meristematic cell. The anatomical environment of this meristematic cell may influence the nature of what develops from it, but we must realize that when this development is complete the resulting structure may be categorically independent of the structure that originally produced the cell. What is important is the nature and identity of this resulting structure.

Through the vagaries of meristematic initiation, such structures may develop anywhere in the organization system. Where the predisposing causes of their synthesis become organized in the gene pattern, they are to be regarded as normally a part of the ontogeny of the plant and may be represented by any tissue, tissue system, or organ, or by modifications or by parts of these. In effect, in their ontogenetic elaborations they constitute organization systems of their own and can be abstractly superimposed upon the general organization system and correlated in a one to one manner with comparable structures as they may occur anywhere on the plant (fig. 1, A′, B′, C′). Thus parenchyma is parenchyma, anywhere on the plant, irrespective of the structure that gives rise to its initiating cell or cells. We may think of it as being related solely to the predisposing causes of parenchyma, whatever that combination of conditions and events may be. Likewise any other structure as it may occur normally or abnormally is to be regarded primarily in terms of what it is rather than the nature of its meristematic origin. What is important in each of these cases is, 'What is the structure that results from such activity?' and not, 'From where did it arise?'

The Concept of Homology

As mentioned above, the concept of homology had its origin among the ancient geometricians and was applied to biology by the anatomical philosophers at the beginning of the last century. In biology it found its first linguistic form in the doctrine of metamorphosis of Wulff and Goethe. Thus homology is not solely a biological notion. It is to Owen (1848) that we turn for most of the current notions of homology as applied in biology. Owen thought of homology as a serial system, although he expressed himself in a manner that introduced some confusion between his serial system and his example, namely the serial segmentation of animals to which he applied the notion. Homologies outside of a given serial system could be drawn wherever the necessary comparisons could be made and relations established. These relations served to connect the serial systems of diverse organisms. This Owen spoke of as establishing general homology. In view of current controversy it appears that some clarification of these notions is in order.

Homology as employed in biology is an adaptation of the notions of set theory, relations theory, and the theory of types, together aimed at establishing the formal relations between the structures of organisms (Woodger, 1937). The relations that we in biology speak of as "homology" differ from ordinary relations because the field of the relations is the

organism, which comprises a dynamic system. The relations thus imply the operations of the dynamic system that have brought them about. So compelling is this implication that to many it has become an integral part of the concept, with the dire consequences that the formality of the relations is often confused by having some anticipated notion of the implication built into it. However, the actual homology rests solely upon the formal relations in the serial system, and these should be established independently of any implication to be derived from them or to be anticipated in their behalf and independently of any explanation that may be forthcoming from our understanding or our misunderstanding.

Serial homology actually is the serial system of class relations in ascending order into which any given structure may be classified. For example, a petal of a flower belongs to the following series of classes:—petal, corolla, perianth, flower part, appendage. Each class level represents an increase in the scope of structures that are included as homologous organs. Each class expresses the homologous relation of its included terms. Thus a leaf and a petal bear the homologous relation "appendage" to one another. Each class at each level comprises a logical type.

One may insert classes or subclasses into this system as occasion may demand so long as they are inserted in a proper serial order determined by the scope of the relations that are expressed. The number of properties and the nature of the properties upon which the class is based is not important. Its position in the series is. This is because each such class stems from the logical conjunction of subclasses, and hence it represents the logical connection of the subclasses in series with the class. We thus have in the system the basis for establishing order and connectedness among the morphological properties of organisms. Through their connectedness their morphological equivalence is implied.

As one approaches the system analytically, it will be found that the basis of the implication accrues by mathematical induction, each subclass at each level adding its increment to the logical type of its predecessor to establish its own logical type. And as each new logical type is thus established, the scope of the relations expressed is thereby narrowed. The compelling feature of the implication is enhanced by the orderliness of these accruing foundations of relations and the realization that they are founded in ontogeny. Also, as they relate to the interpretations of phylogeny they give some semblance of meaning to the biogenetic law in that the properties of each predecessor class must be synthesized in ontogeny as the foundation for the synthesis of the properties of successor classes. This is solely logical implication and not logical proof. The scope of the relations of the more inclusive classes, however, is significant, since it serves to give a sequence of order to the properties.

Because of the complex nature of higher plants, the serial system must be thought of in terms of various structural levels of homology rather than in terms of a single organographic series culminating in the individual as the class that includes all. The organographic series provides a very

incomplete concept of serial homology. It should be clear that homologies are possible on different levels of organization of ontogeny. The cytologist employs the concept at the level of cells and cell contents. Here homologies of very broad scope are possible. The basis of homology rests in the identity of the structure, and it implies origin from a pre-existing similar structure. At a higher level in the system the anatomist employs the concept of homology for tissues and tissue systems. Here like or equivalent cells are organized into tissues arising from a common or equivalent meristem as they become a part of a higher organizational tissue system. In such cases the homology often becomes restricted within the scope of the ontogenetic lineage cut off in the differentiation of the promeristem into protoderm, procambium strands, and ground meristem.

A third level of homology may be spoken of as the organographic level involving identity and positional relations of organs and appendages. Here we are concerned with cells, tissues, and tissue systems constituting organs and appendages as these arise similarly from like meristems and are arranged upon a common plan.

As we ascend the levels of structural complexity, the scope of possible homologies is reduced and becomes more localized as to areas of the plant and involves fewer serial structures. Likewise, in general homology, the higher the organizational level the fewer are the homologies that can be broadly drawn. Thus, on the organographic level one is less able to draw broad homologies than one is on the level of tissues and cells. For instance, carpels are confined to the angiosperms, tracheids are present in several classes of plants, while cells are characteristic of all plants.

Because of the capacity of dividing cells to generate structures morphologically unrelated to the organ that bears them, one must recognize this state of affairs in his concept of homology. It calls for an assessment of the situation in terms of what structures result and how they may be correlated with the organization system as a whole. The homologies of such structures become evident through their identity and their assignment to the proper level in the serial system of the whole. For such homologies I shall use the term "regeneration homology."

Any deviation that is evident in a practical application of this system must seek its explanations in regeneration homology. This will be particularly evident when a structure attains properties assignable to a structure other than that on which it occurs. It will also be evident when a tissue occurs in the confines of a meristem system in which such tissues do not ordinarily arise.

The Need for Clear Definitions

In the practical application of homology to the problems for which the logical system is devised, it becomes imperative that such structures and abstractions employed be clearly as well as inclusively and exclusively defined. The chief problems in establishing homology are precisely traceable to these difficulties of definition or to semantic problems in not under-

standing the level of abstraction and the resulting error as to what criteria are involved. Whereas a sporangium may be significant to the concept "carpel," it is not significant to the concept "appendage" and has nothing to do with the inclusion of carpels as appendages. There may be many other features of carpels that may be significant to the concept of carpel or significant to the carpel of some particular kind of plant, but they play absolutely no role in the abstractions of the category "appendage" which are based upon the common characters of kinds of appendages. We are not concerned with the characters of carpels whereby they may be unlike other appendages. We are only concerned whether or not they possess the characters that are diagnostic of the abstract concept "appendage." To the extent that these characters are present, we classify the carpel as an appendage and to this extent it fulfills the classical theory as amended by Lindley. To this extent also, the assignment of the carpel to the concept "appendage" constitutes another relation step in our logical system. We must be aware, however, that logic is not self-validating, and in this case it is no more valid than is the significance of the criteria of morphological equivalence that we have accepted. The logical system is only a method of handling the facts that we accept as valid. We cannot hold the system responsible for the validity of these facts. Our logic cannot correct our mistakes, although sometimes it may assist in pointing them out.

When we find carpels that display characters that confuse us as to what structural category in which to include them, it seems to me necessary to investigate whether or not we are dealing with a simple situation or with a phenomenon that may be better handled through the logic of regeneration homology. Perhaps the occurrence of sporangia on sporophylls is such a case. Some seem to think that a sporangium is normally terminal on a cauline structure. Should this be true the problem of sporangia on appendages fits naturally into the logical system of regeneration homology. We would presume that through the predisposing causes of ontogeny a meristematic event takes place that generates a sporangium on an appendage, and these facts make of the appendage a sporophyll. When provision for the synthesis of the predisposing causes becomes organized in the gene system, the production of sporangia on appendages is normal. Such an event in no way destroys the homologies of the sporophyll as an appendage. It is in every way comparable to the occurrence of buds on the margin of the leaf of *Bryophyllum*.

I deliberately employed the sporangium in this example because it was easy to discuss and seemed to fit in well as an example. There are other stem-like tissues reported in carpels that have raised questions of their reference to appendages. The explanations of these should be sought upon an anatomical level of homology and evidence sought as to what structures are represented and what has been their ontogenetic history. Next the problem is to find the extent of their organization and what their resulting homologies may be.

The fact that we seek identity in the old does not mean that new struc-

tures might not appear and that new structures are not possible in the gynoecium. It does mean that before we can assign them as being new structures, we must have some criteria other than our confusion in the interpretation of the old, upon which to base our decision. A new structure is one which does not possess the diagnostic criteria that would permit it to be classified in any existing category of structures at the same organization level.

Much of this confusion stems from lack of clarity as to what constitutes any particular organ or structure. For example, much of the problem of the inferior ovary stems from the fact that we do not have an adequate definition of a receptacle drawn from characters that are diagnostic of a receptacle. The result has been that we seek evidence of receptacles in criteria that are not diagnostic of such a structure, as, for example, the employment by Smith (1943) of recurrent bundles in the structures surrounding the ovary in Santalaceae as evidence that this structure is a receptacle. If the structure surrounding the inferior ovary and traversed by the recurrent bundles in the Santalaceae is a receptacle, it must be so on some other evidence, for recurrent bundles are not diagnostic of receptacles, nor are branched or unbranched bundles so diagnostic. In seeking diagnostic criteria for the receptacle, about all that I can find common to the several hundred kinds of flowers I have examined is that the receptacle of all of them bears flower parts and is at least operationally terminal on an axis. I have seen no evidence whatsoever in the vascular system that provides for a universally applicable set of criteria by which one might recognize a receptacle as different from any other structure related to stems. We must bear in mind that the plant does not define "receptacle." We as humans define it, and we define it for our own devices.

On the Role of the Telome

If the telome-mesome complex is significant in the interpretations of morphology, it cannot be employed in any problem of diagnostic comparison that employs the logic of homology above the level of meristem differentiation in the organization system. This is because the telome, like the cell, is a ubiquitous structure. It is presumed to be a characteristic of everything and therefore cannot be diagnostic of anything. The logic of homology follows strictly the pattern of diagnostic comparison. To be significant, an attribute must be diagnostic. The cell is significant to homology only on a cytological level where cells are compared with cells. If the telome is significant to homology, it can be significant only on levels where telomes are significant to the diagnosis of the structure. It may be possible to make such diagnoses on the basis of kinds of telome systems if these are valid structures.

Conclusion

This reorganization of our logical system I believe will give us at least a sound working hypothesis for the flower which we can use in developing

our concepts of phylogenetic taxonomy. The concept of homology, because of its ontogenetic implications and because phylogeny also has ontogenetic implications, provides us with the necessary basis for handling the problems of likenesses and differences as they involve comparable structures. There is no problem of phylogenetic divergence, as it is subject to investigation in taxonomy, that is not pursued from the point of view of the logic of the concept of homology as it relates to the properties of organisms.

When we turn from the plant to contemplate what we have seen and to interpret its significance, we must inevitably rely either upon the intuitive judgments of what appear to be immediately self-evident facts, or we automatically resort to a logical system based upon reasoning. The one is the intellectual foundation of sight recognition, the other the intellectual foundation of identification. Both have an important place in interpretive science. Neither is self-validating and therefore either may lead to erroneous judgments. The security of the one rests in the validity of the immediate self-evidence. The security of the other, as it relates to our problem, rests first in the validity of the logical system and then in the validity of the diagnostic criteria.

It therefore becomes important that we develop an adequate logical system such as we strive for in perfecting the system of homology. It is also important that we seriously re-examine the validity of the diagnostic criteria of the structures and the abstractions that we employ as significant to our interpretations. Upon this will rest the validity of their self-evidence, so important to our intellectual manipulations.

We must not assume that simply because we may have more detailed and complete facts, as important as this is, that we can avoid operating within the framework of intuitive judgment and logical systems in our interpretation. If we had all of the facts of structure and ontogeny, we would only shift in our intellectual contemplation of them from a preponderant leaning upon logical systems to a heavier reliance upon intuitive judgment. This is because sight recognition would play a greater role. The validity of our judgments will still rest upon individual human capacities for discrimination as to significance. We still will be plagued by the curse of him who, without understanding them, employs the faulty judgments made by himself or others. The plant is responsible for what is there. What the plant and its structures mean to us is our responsibility, and it is not solely a responsibility of discovery, important as this is, because discoveries must be interpreted to be understood.

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Literature Cited

Boke, Norman H. 1947. Development of the adult shoot apex and floral initiation in Vinca rosea L. Am. Jour. Bot. 34: 433–439.

Cuvier, Georges. 1800. Leçons d'anatomie comparée. Tome i, ii. Paris.

Goethe, J. W. 1790. Versuch die Metamorphose der Pflanzen zu erklaeren. Gotha.

Gregoire, V. 1938. La morphogénèse et l'autonomie morphologique de l'appareil floral. I. Le carpelle. La Cellule 47: 287–452.

Haeckel, Ernst H. P. A. 1876. The history of creation. Transl. by E. Ray. New York.

Lam, H. J. 1948. Classification and the new morphology. Acta Biotheoretica 8: 107–158.

Lindley, J. 1838. Botany. Library of Useful Knowledge. London.

Oken, Lorenz. 1807. Programm, über die Bedeutung der Schädelknochen. Jena.

Owen, Richard. 1848. The vertebrate skeleton. London.

Samassa, Paul. 1896. Caspar Friedrich Wulff's Theoria Generationis. Leipzig.

Smith, Frank H. & Smith, E. C. 1943. Floral anatomy of the Santalaceae and some related forms. Oregon State Monographs, Studies in Botany. The College Press. Corvallis.

St. Hilaire, Geoffrey. 1807. Considérations sur les pièces de la tête osseuse des animaux vertèbres, et particulièrement sur celles du crâne des oiseaux. Ann. Mus. Hist. Naturelle, Paris. 10: 342–365.

Thomas, H. H. 1934. The nature and origin of the stigma. A contribution towards a new morphological interpretation of the angiosperm flower. New Phytol. 33: 173–198.

Thompson, J. M. 1935. The acarpous nature of modern flowering. Proc. Sixth Internat. Bot. Congress 2: 122–124.

Woodger, J. H. 1929. Biological principles. New York.

———. 1937. Axiomatic method in biology. Cambridge Univ. Press.

Zimmermann, Walter. 1930. Die Phylogenie der Pflanzen, ein Überblick über Tatsachen und Probleme. Jena.

MITOTIC CHROMOSOME STUDIES IN THE GENUS ASTRAGALUS[1]

S. Conrade Head

The genus *Astragalus* L., tribe Galegeae of the Leguminosae, consists of about 1,500 species occurring in northern Africa, Europe, northern and central Asia, and in the western hemisphere. Some sixty genera have been proposed as segregates from it, and several taxonomic revisions of the genus or parts of it for North America, based on morphological characters, have been presented (Jones, 1923; Rydberg, 1929; Barneby, 1945, 1947, 1949, 1956). Of these, the more conservative treatments of Jones and Barneby have been found more practical for the purposes of this study.

Very little, however, is known about the cytology of this genus. According to Senn (1938), "Only two per cent of the species of the huge genus *Astragalus* have been studied. These species are based on an 8 series with

[1] This paper represents a portion of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Botany at the State College of Washington, Pullman. 1955.

two exceptions in which n=14. There are 16 diploids, 1 tetraploid, 2 hexaploids, and 1 octaploid. Considering that the species studied come from widely separated regions scattered over Europe and Asia, this is a remarkable consistency of chromosome number." According to Tischler (1938), the findings of ten workers for forty-four Old World species and four New World species were: 2n=16, thirty-three species; 2n=32, three species; 2n=48, four species; 2n=64, five species; 2n=28, 36 and 96, one species each. Vilkomerson (1943) made a survey of twenty-six species from western United States and found that for eleven 2n=24, for thirteen 2n=22, whereas the other two had 2n numbers of 16 and 44 respectively. James (1951) gave chromosome counts for three species, one each of 2n=22, 24 and 26. These several surveys account for approximately one hundred species of *Astragalus*. Certainly the consistent chromosome number stressed by Senn no longer holds. It was with the thought of adding to the chromosomal information for this genus that the present investigation was undertaken.

The author wishes to express his appreciation to Dr. Adolph Hecht, who served as advisor during the course of the research and who with Dr. Marion Ownbey kindly offered many suggestions during the preparation of the manuscript. Mr. Robert C. Barneby provided several of the collections reported here and checked many of the determinations. Mr. Ralph D. Amen offered many valuable suggestions concerning cytological methods.

Methods

The *Astragalus* collections studied are listed by species in Table 1. The source of the collection, the chromosome number, and the figure number (for those collections illustrated) are given. Voucher specimens are filed in the Herbarium of the State College of Washington.

The plants were grown in the greenhouse and later transplanted to an experimental garden at Pullman, Washington. Seeds had to be scarified either by filing or by use of concentrated sulfuric acid, with treatment in the acid from forty-five minutes to one hour being most satisfactory. The scarified seeds were placed on wet filter papers in Petri dishes until the primary root had reached a length of about fifteen mm.; the root was then removed and placed in Belling's "metaphase" modification of Navashin's solution. Root tips were also obtained from pot-bound plants. Some plants were transplanted from their natural habitat to the greenhouse and later to the garden. Since most persons preparing herbarium specimens rarely collect mature fruits, herbarium sheets did not prove to be a profitable source of seed. A few seeds were obtained from herbarium sheets, however, and those as old as nine years germinated without great difficulty provided they were mature when collected.

Paraffin sections cut at twelve microns as recommended by Senn were prepared and stained by the crystal violet-iodine method. These preparations were not as satisfactory as those obtained by a method worked out

by Amen (unpublished).[2] This method provides excellent permanent slides with the cells separated from each other. One has little difficulty in viewing separated cells under the microscope, and the observer is certain that the cells are uncut. Amen plans to publish his method in detail. My modification of his procedure is as follows:

Fix cut root tips in Belling's "metaphase" modification of Navashin's solution preferably for at least two days; remove, rinse several minutes in tap water, blot off excess water; place on slide in one drop of Haupt's adhesive; cut apical 2 mm. into several pieces and squash, using flat side of scalpel; air dry slide about 15 minutes; stain in 1 per cent methyl violet for 10 minutes, wipe off excess stain and nearly air dry; wash momentarily and again nearly air dry; place in solution of 8 grams of picric acid powder dissolved in 1 liter of 95 per cent alcohol for about 20 seconds; blot excess 1 to 2 seconds, place in absolute alcohol about 20 seconds; clear in 50 parts absolute alcohol, 25 parts xylene, and 25 parts clove oil for 3–7 minutes; pass through 2 changes of xylene; mount in piccolyte.

Slides were examined and camera lucida drawings were made of the metaphase plates using a Zeiss microscope with an apochromatic oil-immersion lens of N. A. 1.30 and an initial magnification of 2,250 times. The figure were drawn at approximately 4,350 times and reduced to 1,450 times in reproduction.

Table 1. Chromosome Numbers of Astragalus Collections Studied

Species	Chromosome Number (2n)	Figure Number	Source
Section Homalobi[3]			
A. stenophyllus T. & G.	24	1	Oregon, Morrow County: 12.9 miles southwest of Heppner, *Head 598.*
	24	2	Oregon, Baker County: 12.5 miles southeast of Baker on the Ebell Creek Road, *Head 609.*
	24	3	Oregon, Wheeler County: 16 miles south of Condon, *Head 600.*
Section Inflati			
A. lentiginosus Dougl. ex Hook. var. *lentiginosus*	22	4	Oregon, Baker County: 1 mile east of Quartz, *Head 607.*
A. cusickii A. Gray	22	5	Washington, Asotin County: near the Grande Ronde River bridge, *Head 569.*
	22, 44*[4]	36	Oregon, Baker County: 13 miles west of Richland, *Head 611.*

[2] Amen, Ralph D., former graduate student, State College of Washington. Present address: 2426 South University, Denver, Colorado.

[3] Sections are those listed by Jones (1923) although this arrangement is not always satisfactory.

[4] Diploid and tetraploid cells occur in the same root tip of many Leguminosae. See discussion on polysomaty. Such counts are indicated by an asterisk.

Species	Chromosome Number (2n)	Figure Number	Source
A. beckwithii T. & G. var. *weiserensis* M. E. Jones	22	6	Idaho, Owyhee County: 10 miles north of Silver City, on road to Murphy, *Christ 19537.*
A. allochrous A. Gray	22	7	New Mexico, Grant County: San Lorenzo, *Barneby 11172.*
Section Collini			
A. collinus (Dougl. ex Hook.) G. Don var. *collinus*	24, 48*	8, 37	Washington, Asotin County: 5.5 miles northeast of Anatone, *Head 585.*
	24	9	Washington, Asotin County: 6.3 miles northeast of Anatone, *Head 588.*
var. *laurentii* (Rydb.) Barneby	24	10	Oregon, Morrow County: 18.6 miles east of Heppner, *Head 596.*
Section Hamosi			
A. andersonii A. Gray	24	11	Nevada, Washoe County: 6 miles northwest of Univ. of Nevada Campus, Reno, *Ownbey 2925.*
A. arthurii M. E. Jones	24	12	Washington, Asotin County: 3.4 miles northeast of Anatone, *Head 587.*
A. congdonii S. Wats.	26, 52*	13, 39	California, Fresno County: Piedra, *Barneby 11417.*
Section Podo-Sclerocarpi			
A. sclerocarpus A. Gray	22	14	Washington, Benton County: 2 miles west of Enterprise (West Richland), *Head 525.*
A. pachypus Greene	22	15	California, Kern County: Caliente, *Barneby 11370.*
Section Reventi-arrecti			
A. arrectus A. Gray	24	16	Washington, Whitman County: Prairie Strip, Botany Dept. State College of Washington, Pullman, *Head 584.*
A. sheldonii (Rydb.) Barneby	24	17	Washington, Asotin County: 3.4 miles northeast of Anatone, *Head 586.*
A. riparius Barneby	24	18	Washington, Whitman County: 3.3 miles northeast of Wawawai, *Head 562.*

Species	Chromosome Number (2n)	Figure Number	Source
	24	19	Washington, Whitman County: 1.1 miles east of Wawawai, *Head 563.*
A. conjunctus S. Wats.	24	20	Oregon, Wheeler County: 16 miles south of Condon, *Head 599.*
A. eremeticus Sheldon var. *malheurensis* (Heller) Barneby	24	21	Idaho, Washington County: just north of Weiser, *Ownbey 2761.*
Section Uliginosi			
A. canadensis L. var. *mortonii* (Nutt.) S. Wats.	16	22	Washington, Whitman County: north slope of Kamiak Butte, *Head 613.*
Section Chaetodontes			
A. spaldingii A. Gray	24	23	Washington, Whitman County: ½ mile east of Lacrosse, *Head 582.*
Section Argophylli			
A. inflexus Dougl. ex Hook.	22	24	Washington, Whitman County: 1 mile northeast of Wawawai, *Head 499.*
A. purshii Dougl. ex Hook. var. *glareosus* (Dougl. ex Hook.) Barneby	22, 44*	25, 38	Oregon, Baker County: 1 mile east of Quartz, *Head 547.*
	22	26	Oregon, Morrow County: 18.6 miles east of Heppner, *Head 595.*
	22	27	Oregon, Grant County: 2.5 miles north of Mt. Vernon, *Head 603.*
	22	28	Oregon, Grant County: 2.4 miles north of Mt. Vernon, *Head 604.*
var. *purshii*	22	29	Washington, Whitman County: top of Steptoe Butte, *Head 580.*
A. chamaeleuce A. Gray	22	30	Colorado, Mesa County: 3 miles south of Fruita, *Weber 3782.*

Species	Chromosome Number (2n)	Figure Number	Source
A. cibarius Sheldon	22	31	Idaho, Bannock County: 12 miles south of Portneuf, *Christ 19933.*
Section Malaci			
A. succumbens Dougl. ex Hook.	24	32	Washington, Walla Walla County: 7.4 miles east of Wallula, *Head 539.*
Section Mollissimi			
A. mollissimus Torr. var. *earlei* (Rydb.) Tidest.	24	33	Texas, Jeff Davis County: southeast of Fort Davis, *Barneby 11129.*
Section Sarcocarpi			
A. gypsodes Barneby	24	35	New Mexico, Eddy County: southwest of Whites City, *Barneby 11138.*
Section undetermined			
A. diaphanus Dougl. ex Hook.	28	34	Oregon, Wheeler County: 2 miles east of Service Creek, *Hitchcock 19235.*

Discussion

As the table indicates, chromosome numbers of 2n=16, 22, 24, 26, and 28 were found in the plants studied. The sections *Inflati, Collini, Podo-sclerocarpi, Reventi-arrecti* and *Argophylli* showed constant chromosome numbers. The section *Hamosi* had two different chromosome numbers represented; *A. andersonii* and *A. arthurii* both had 2n=24, and *A. congdonii,* 2n=26. A like situation was reported by Vilkomerson (1943) for the section *Galegiformes.* Even prior to her publication, the need for a taxonomic revision considering physiological evidence was suggested by Trelease (1942). Vilkomerson also reported a chromosome number of 2n=22 for *A. crassicarpus* Nutt.; *A. gypsodes* is recorded above as having 2n=24. Barneby (1956) groups these two species together in the same section. James (1951) found three different chromosome numbers represented by three species in the section *Didymocarpi.* Thus we see it is possible for a section to have species with different chromosome numbers. Yet, as cytological information accumulates for the genus, more sections are found to have a constant chromosome number. Much more study is needed in the section *Hamosi* and, as Trelease mentioned, in the *Galegiformes.*

Certain species of *Astragalus* can be readily identified by their characteristically shaped chromosomes. Among these are *A. succumbens* with a pair of large "question mark" chromosomes and *A. mollissimus* var. *earlei*

with its eight pairs of "C" chromosomes. The sections *Reventi-arrecti* and *Argophylli* may also be recognized by chromosome similarities of the included species.

Figs. 1–20. Chromosomes of *Astragalus*. 1–3, *A. stenophyllus*; 4, *A. lentiginosus* var. *lentiginosus*; 5, *A. cusickii*; 6, *A. beckwithii* var. *weiserensis*; 7, *A. allochrous*; 8–9, *A. collinus* var. *collinus*; 10, *A. collinus* var. *laurentii*; 11, *A. andersonii*; 12, *A. arthurii*; 13, *A. congdonii*; 14, *A. sclerocarpus*; 15, *A. pachypus*; 16, *A. arrectus*; 17, *A. sheldonii*; 18–19, *A. riparius*; 20, *A. conjunctus*. Camera lucida drawings, × 1450.

Section Homalobi (figs. 1–3, idiograms 1–3).—Geographical distribution of *A. stenophyllus* appears to have little correlation with chromosome morphology in this species. Figures 2 and 3 are from plants which grew about two hundred miles apart, yet the chromosomes appear more alike than those of figures 1 and 3 which are from plants separated by only a few miles.

Section Inflati (figs. 4–7, 37; idiograms 4–7).—In all of the *Inflati* so far studied the 2n number is 22, provided *A. diaphanus* is not referred here. However, the section as a whole cannot be characterized or identified on the basis of chromosome similarity, for the positions of the centromeres are not as consistent as in those groups already mentioned. Both *A. allochrous* and *A. cusickii* have four pairs of chromosomes with nearly median centromeres which take a characteristic "C" shape. *A. beckwithii* var. *weiserensis* has but one pair of these chromosomes. *Astragalus allochrous* (fig. 7) has the largest chromosomes of any found in this study.

Section Collini (figs. 8–10, idiograms 8–10).—In contrast to the low correlation of chromosome morphology with geographical distribution in *A. stenophyllus* of section *Homalobi,* here there is much similarity in chromosome morphology from plants separated by even greater distances.

Section Hamosi (figs. 11–13, idiograms 11–13).—The two species with the 24 chromosomes, *A. arthurii* and *A. andersonii,* have little in common with the 26 chromosome species *A. congdonii.* The latter (fig. 13) has five pairs of "C"-shaped chromosomes, while the former two species have only two pairs. *Astragalus arthurii* is unique in that one chromosome (the last in idiogram 12) shows a prominent constriction at about the middle, which might be the centromere region. Chromosomal data beyond that now available should be obtained before a revision of the *Hamosi* is attempted.

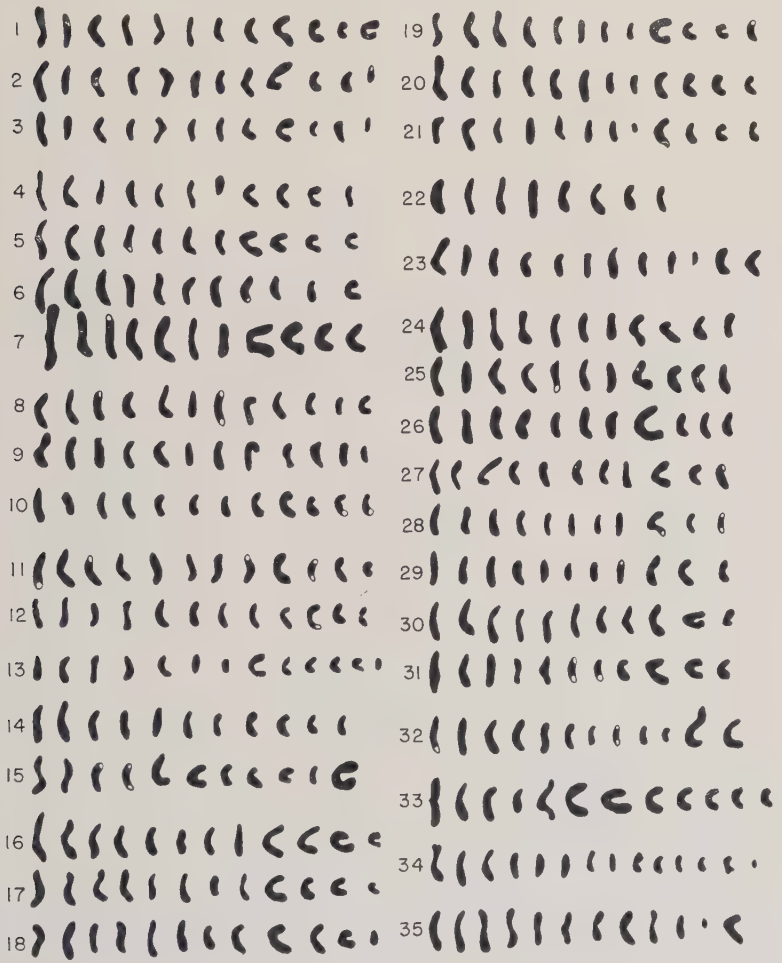
Section Podo-sclerocarpi (figs. 14–15, idiograms 14–15).—Vilkomerson studied nine species belonging here, including *A. sclerocarpus,* and found the same chromosome number (2n=22) in all. *A. pachypus* is the only new report for a species of this section. Unlike *A. sclerocarpus* (idiogram 14), *A. pachypus* (idiogram 15) has several pairs of "C"-shaped chromosomes.

Section Reventi-arrecti (figs. 16–21, idiograms 16–21).—Members of this section have very similar chromosomes. Each of the five species studied has four pairs of "C"-shaped chromosomes. Although these chromosomes vary somewhat in length they are otherwise very similar. *Astragalus eremeticus* var. *malheurensis* (idiogram 21) differs somewhat from the others by having a pair of small "dot" chromosomes not found elsewhere in this section.

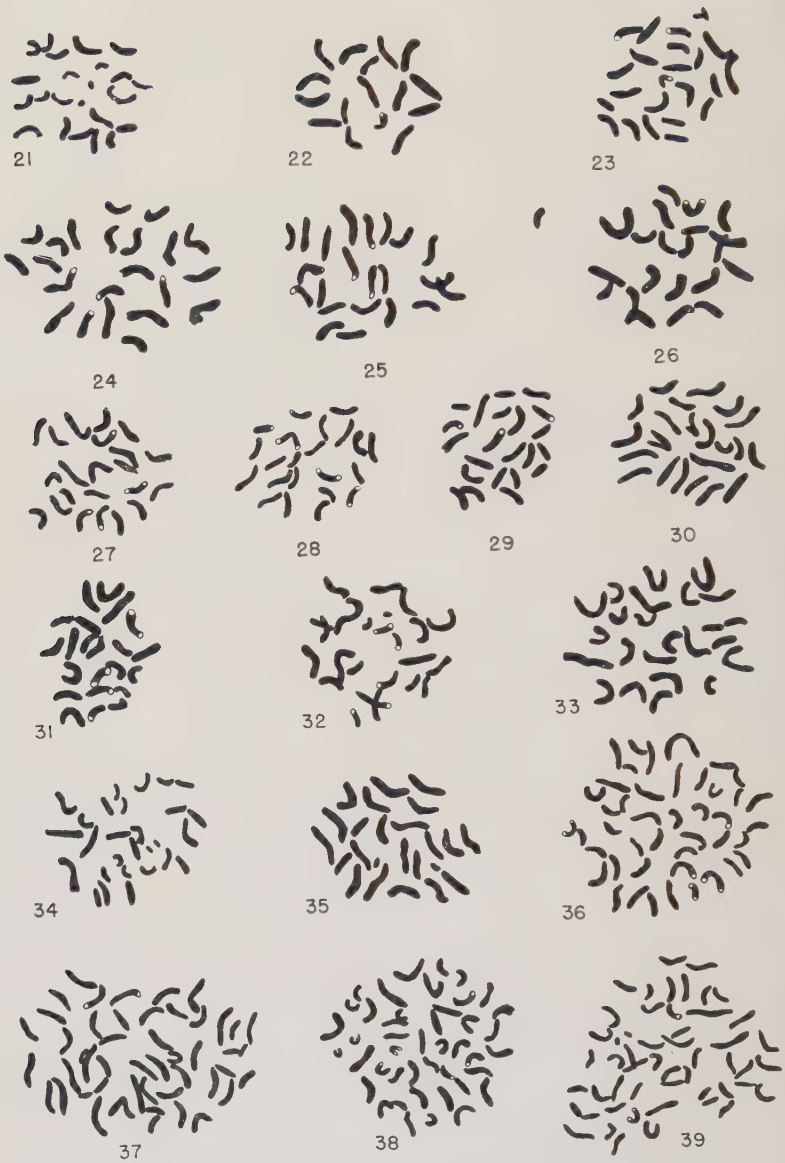
Section Uliginosi (fig. 22, idiogram 22).—Only one species of the *Uliginosi* has been studied, *A. canadensis* L., reported by Vilkomerson, and *A. canadensis* var. *mortonii* of this study.

Section Chaetodontes (fig. 23, idiogram 23).—*A. spaldingii* is the only member of this section thus far studied.

Section Argophylli (figs. 24–31, 38; idiograms 24–31).—The *Argophylli,* as a section, show a close likeness in chromosome morphology and number. This similarity is perhaps to be expected with closely related species such as *A. inflexus* and *A. purshii,* but it would not necessarily



Idiograms 1–35. Chromosomes of *Astragalus.* 1–3, *A. stenophyllus*; 4, *A. lentiginosus* var. *lentiginosus*; 5, *A. cusickii*; 6, *A. beckwithii* var. *weiserensis*; 7, *A. allochrous*; 8–9, *A. collinus* var. *collinus*; 10, *A. collinus* var. *laurentii*; 11, *A. andersonii*; 12, *A. arthurii*; 13, *A. congdonii*; 14, *A. sclerocarpus*; 15, *A. pachypus*; 16, *A. arrectus*; 17, *A. sheldonii*; 18–19, *A. riparius*; 20, *A. conjunctus*; 21, *A. eremeticus* var. *malheurensis*; 22, *A. canadensis* var. *mortonii*; 23, *A. spaldingii*; 24, *A. inflexus*; 25–28, *A. purshii* var. *glareosus*; 29, *A. purshii* var. *purshii*; 30, *A. chamaeleuce*; 31, *A. cibarius*; 32, *A. succumbens*; 33, *A. mollissimus* var. *earlei*; 34, *A. diaphanus*; 35, *A. gypsodes.* Camera lucida drawings, × 1450.



Figs. 21–39. Chromosomes of *Astragalus*. 21, *A. eremeticus* var. *malheurensis*; 22, *A. canadensis* var. *mortonii*; 23, *A. spaldingii*; 24, *A. inflexus*; 25–28, *A. purshii* var. *glareosus*; 29, *A. purshii* var. *purshii*; 30, *A. chamaeleuce*; 31, *A. cibarius*; 32, *A. succumbens*; 33, *A. mollissimus* var. *earlei*; 34, *A. diaphanus*; 35, *A. gypsodes*; 36, *A. cusickii*; 37, *A. collinus* var. *collinus*; 38, *A. purshii* var. *glareosus*; 39, *A. congdonii*. Camera lucida drawings, × 1450.

extend to such distant species as *A. chamaeleuce* from Colorado or to *A. cibarius* from southeastern Idaho. It would be interesting to determine if this similarity is maintained throughout this large section. *Astragalus cibarius* is excluded from the *Argophylli* by Barneby (1947), and he suggests a relationship with the *Malaci* for this species. On the basis of chromosome morphology and number, however, it seems very much like the other *Argophylli* and very little like the only representative of the *Malaci, A. succumbens,* thus far studied.

Section Malaci (fig. 32, idiogram 32).—*Astragalus succumbens* has one pair of large "C"-shaped chromosomes and a pair of "question mark"-shaped chromosomes.

Section Mollissimi (fig. 33, idiogram 33).—*Astragalus mollissimus* var. *earlei* has eight pairs of "C"-shaped chromosomes.

Section Sarcocarpi (fig. 35, idiogram 35).—*Astragalus gypsodes* has 11 pairs of relatively long chromosomes and 1 pair of very short ones.

Astragalus diaphanus (fig. 34, idiogram 34) has not been determined as to section. This species stands alone among the North American species studied in that the 2n chromosome number is 28. The chromosomes are also the smallest observed in this study. Jones (1923) listed *A. diaphanus* as a variety of *A. lentiginosus,* a member of his section *Inflati.* Barneby (1945) excluded *A. diaphanus* from his section *Diplocystium* (composed of the varieties of *A. lentiginosus*), but did not propose a new status. *A. diaphanus* should be excluded from the *Inflati* on the bases of chromosome number and fruit morphology. These reasons also support Barneby's exclusion of it from the *Diplocystium.*

Polysomatic Cells. In *Astragalus,* as in many other genera of the Leguminosae, both diploid and tetraploid cells may be found in the same root tip. Vilkomerson reported polysomaty in three species, but listed its occurrence as rare. Polysomatic cells were found by Tschechow (1930) in two of the species he studied. In one of these, *A. candidissimus,* tetraploid cells were found in forty per cent of the metaphase plates. Polysomatic cells were observed in four of the taxa of the present study: *A. cusickii, A. purshii* var. *glareosus, A. collinus* var. *collinus,* and *A. congdonii* (figures 36, 37, 38 and 39). In the last three species the occurrence of such cells are rare, but *A. cusickii* had about the same percentage of tetraploid cells found by Tschechow in *A. candidissimus.*

Summary

Mitotic chromosome studies were made of twenty-six species of *Astragalus* represented by thirty-five collections. The 2n chromosome numbers of 16, 22, 24, 26 and 28 were found. The basic number of 14 is added to those previously reported for the North American species. Chromosome numbers for species of the sections *Homalobi, Collini, Hamosi, Reventiarrecti, Argophylli, Chaetodontes, Malaci* and *Mollissimi* are reported for the first time. Counts for three species substantiate those previously published. Certain species and some sections of the genus can be readily rec-

ognized on the basis of chromosome morphology. *Astragalus diaphanus* should be excluded from the *Inflati* on the basis of chromosome number and morphology.

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Literature Cited

Barneby, R. C. 1945. Pugillus Astragalorum IV: The section Diplocytium. Leafl. West. Bot. 4:65–147.
———. 1947. Pugillus Astragalorum VII: A revision of the Argophylli. Am. Midl. Nat. 37:421–516.
———. 1949. Pugillus Astragalorum X: New species, varieties and combinations. Am. Midl. Nat. 41:496–502.
———. 1956. Pugillus Astragalorum XVIII: Miscellaneous novelties and reappraisals. Am. Midl. Nat. 55:477–503.
James, Lois E. 1951. Observations on the taxonomy of Astragalus, subgenus Hesperastragalus. Contr. Dudley Herb. 4:63–72.
Jones, M. E. 1923. Revision of North-American species of Astragalus. Salt Lake City, Utah.
Rydberg, P. A. 1929. "Astragalanae" in N. Am. Flora 24:251–462.
Senn, Harold A. 1938. Chromosome number relationships in the Leguminosae. Bibliographia Genetica 12:175–336.
Tischler, G. 1938. Pflanzliche Chromosomen-zahlen. IV. Tabulae Biologicae 16: 162–218.
Trelease, Sam F. 1942. Identification of selenium indicator species of Astragalus by germination tests. Science 95:656–657.
Tschechow, W. 1930. Karyologisch-systematische Untersuchung des Tribus Galegeae Fam. Leguminosae. Planta 9:673–680.
Vilkomerson, Hilda. 1943. Chromosomes of Astragalus. Bull. Torrey Club 70: 430–435.

INNOVATIONS IN DUDLEYA

Reid Moran

As a thesis at the University of California, I prepared a revision of *Dudleya* (Crassulaceae). This revision is not yet ready for publication and may not be ready for several years. Meanwhile, two floras including *Dudleya* are nearly completed, and there is immediate need for certain names from the thesis. Therefore, one new subspecies will be described and several new combinations proposed. Abbreviations for the names of herbaria are according to Lanjouw and Stafleu (1956).

Dudleya abramsii Rose subsp. **murina** (Eastwood) Moran, comb. nov. *Dudleya murina* Eastwood, Proc. Calif. Acad. IV. 20: 147. 1930.

Dudleya cymosa (Lemaire) Britton & Rose subsp. **gigantea** (Rose) Moran, comb. nov. *Dudleya gigantea* Rose in Britton & Rose, Bull. N.Y. Bot. Gard. 3: 23. 1903.

Dudleya cymosa (Lemaire) Britton & Rose subsp. **marcescens** Moran, subsp. nov. A subspeciebus ceteris caudicibus tenuioribus, rosulae

foliis minoribus aestate marcescentibus, inflorescentiis simplicioribus differt (fig. 1).

Caudex 1–3 cm. long, 2–7 mm. thick, often branching; rosettes 3–6 cm. wide, of 8–12 (–15) leaves; rosette leaves green, oblanceolate, acute to subobtuse, 1½–3 (–4) cm. long, 5–12 mm. wide, 1–2 mm. thick; floral stems 4–10 cm. tall, their leaves deltoid-lanceolate, ½–1½ cm. long; inflorescence of 1–2 cincinni, each 1–3 cm. long and with 2–5 flowers; pedicels erect, 5–12 mm. long; sepals deltoid, acute, 2½–4 mm. long; petals bright yellow often marked with red, 10–14 mm. long, 2½–3½ mm. wide, connate ca. 1½ mm.

FIG. 1. *Dudleya cymosa* (Lemaire) Britton & Rose subsp. *marcescens* Moran, subsp. nov. (type collection) × 0.6.

Type: Shaded rocky slope by the creek, Little Sycamore Canyon, Sierra Santa Monica, Ventura County, California (near 34° 05′N, 118° 57′W), at about 330 meters elevation, May 28, 1948, *Moran 3078* (UC 917950).

Specimens examined: known only from the type locality, Little Sycamore Canyon, *Moran 1890* (CU), *2072* (UC), *3078* (type: UC; isotypes DS, POM).

Illustration: Des. Pl. Life 8: 70. 1936. The plant shown in this photograph is very lax, apparently as a result of cultivation.

Uhl and Moran (1953, p. 495, under *Dudleya* sp. affin. *D. ovatifolia*) reported a gametic number of 17 chromosomes in each of two collections of *D. cymosa marcescens*. Thus, like the other subspecies of *D. cymosa,* this plant is diploid with relation to the basic number for the genus.

The subsp. *marcescens* appears to be the most distinctive of the subspecies recognized here for *D. cymosa*. It is quite different from the subsp. *cymosa,* of central California, but in some respects these two are connected by the subsp. *ovatifolia,* which also occurs locally in the Sierra

Santa Monica. The subsp. *marcescens* appears to be quite distinct from the subsp. *ovatifolia,* differing in its more slender caudex, in its narrower rosette leaves, and in the withering of its rosette leaves in summer.

The only other member of the subgenus *Dudleya* known to be completely leafless in summer is *D. parva* Rose & Davidson. That also is a small diploid plant very local in Ventura County: it occurs about 8 miles north of Little Sycamore Canyon. *Dudleya parva* is quicker to lose its leaves in summer and slower to produce new ones after the first rains. It differs from *D. cymosa marcescens* further in its narrower rosette leaves, its much shorter pedicels, and its less sharply acute petals, which are pale yellow rather than bright yellow. For description and photographs of *D. parva,* see Moran, 1948.

Dudleya cymosa (Lemaire) Britton & Rose subsp. **minor** (Rose) Moran, comb. nov. *Dudleya minor* Rose in Britton & Rose, Bull. N. Y. Bot. Gard. 3: 19. 1903.

Dudleya cymosa (Lemaire) Britton & Rose subsp. **ovatifolia** (Britton) Moran, comb. nov. *Dudleya ovatifolia* Britton in Britton & Rose, Bull. N. Y. Bot. Gard. 3: 20. 1903.

Dudleya cymosa (Lemaire) Britton & Rose subsp. **setchellii** (Jepson) Moran, comb. nov. *Cotyledon laxa* (Lindley) Brewer & Watson var. *setchellii* Jepson, Fl. West. Mid. Calif. 267. 1901.

Dudleya hassei (Rose) Moran, comb. nov. *Stylophyllum Hassei* Rose in Britton & Rose, Bull. N. Y. Bot. Gard. 3: 35. 1903.

Dudleya saxosa (M. E. Jones) Britton & Rose subsp. **aloides** (Rose) Moran, comb. nov. *Dudleya aloides* Rose in Britton & Rose, Bull. N. Y. Bot. Gard. 3: 15. 1903.

Dudleya saxosa (M. E. Jones) Britton & Rose subsp. **collomiae** (Rose) Moran, comb. nov. *Dudleya Collomae* Rose in Morton, Des. Pl. Life 6: 68. 1934.

San Diego Natural History Museum,
San Diego, California.

Literature Cited

Lanjouw, J., and F. A. Stafleu. 1956. Index herbariorum. Part I, the herbaria of the world. Ed. 3. Utrecht

Moran, Reid. 1948. Dudleya parva, Rose & Davidson. Des. Pl. Life 20: 137–140.

Uhl, Charles, and Reid Moran. 1953. The cytotaxonomy of Dudleya and Hasseanthus. Am. Jour. Bot. 40: 492–502.

NOTES AND NEWS

Cleistogamy in Mimulus Douglasii Gray. In 1938, J. T. Howell described a small cleistogamous-flowered *Mimulus* as *M. cleistogamus* (Leafl. West. Bot. 2: 79), but he later (op. cit. 3: 127–128. 1942) recognized it as merely a "growth phase" of *M. Douglasii.* My own observations indicate the frequent presence of cleistogamous flowers in *M. Douglasii.* Their presence seems to be related to absence of sufficient water in the soil. Normally these plants grow in thin soil over sandstone, and, in years when late winter and early spring rains come often enough, they produce large open flowers. In some situations, for example, where the soil is extremely thin on

southern exposures, this seldom happens, and year after year, only cleistogamous flowers are produced.

A colony was once seen where apparently the water supply was cut down at a critical moment, following which some of the plants produced small open flowers some of which were abnormal for *M. Douglasii* (*V. F. Hesse 918,* Jepson Herbarium, University of California, Berkeley). One of these small flowers was observed to resemble in shape the flowers of *M. Congdonii* Robinson. Although *M. Congdonii* grows in the same area, it apparently requires a somewhat deeper soil, and has not been observed to produce cleistogamic flowers. These observations were made in the Boulder Creek area of Santa Cruz County. —V. F. Hesse, Boulder Creek, California.

Notes on California Grasses. Three summer weedy annual grasses are extending their range northward in California. They occur on wet soils, periodically flooded by irrigation during the summer months. Specimens cited are at the Agronomy Herbarium, University of California, Davis.

1. Eriochloa contracta Hitchc. (prairie cupgrass). Generally of sparse occurrence in the state. Introduced from the Great Plains originally into southern California. William H. Allison collected the grass in Merced County in 1939 and the author discovered it in northern Solano and southern Yolo counties (*Crampton 3147, 3148*) in the summer of 1955. Apparently well-established here and competing successfully with *Echinochloa crus-galli* and *Echinochloa colonum.*

2. Chloris virgata Swartz (feather fingergrass). Occurs mostly in southern California and the San Joaquin Valley. Collection of the grass from near Davis, Yolo County (*Crampton 3140*), and Pentz, Butte County (*Morse,* Farm Advisor, Butte County), confirms its northward extension. The plant has been reported seen near Auburn, Placer County, but no voucher is available.

3. Leptochloa fascicularis (Lam.) Gray (sprangletop). This is now a very common weedy grass preferring wet habitats ranging from loose, sandy soils of stream and river shores to heavy adobe or alkaline soils of valley plains and river bottomlands. In its early development, the grass probably behaves as an aquatic, since maturing plants are often partially immersed in water, particularly in and around rice fields. Distribution of the grass in California may be designated as follows:

Infrequent: in the Coast Ranges from San Francisco Bay south to Lower California; alkaline soils east of the Sierran Crest from Lassen County south to Inyo County. Abundant: Great Valley, Butte County south to Kern County.

Agrostis tandilensis (O. Kuntze) Parodi (*A. kennedyana* Beetle). This rare annual grass, previously known in California only from San Diego County, was discovered in Solano County (*Crampton 3275, 3289, 3296, 3300*) during April, 1956. The general area of occurrence of this species begins about 7.5 to 8 miles south of Dixon, on the road to Rio Vista, centers around Dozier Station, and extends southward for several miles. The area habitat is one of a valley plain with low and small to large hummocks interspersed with hog wallows or vernal pools that are largely alkaline and support tufts of the rhizomatous *Distichlis* along with *Eryngium, Deschampsia danthonioides, Baeria,* and *Pogogyne.* The hummocks support largely the Mediterranean annual grasses *Bromus mollis, Bromus rigidus, Festuca bromoides* and close allies, *Avena barbata, Hordeum hystrix,* and *Lolium multiflorum.* In some localized areas, the vestiges of the old Pacific Bunchgrass region is seen in *Stipa pulchra* and the less common *Melica californica.* Some native Trifoliums are in abundance, particularly the striking *Trifolium barbigerum* var. *lilacinum* (Greene) Jepson.

Agrostis tandilensis is relatively inconspicuous in the beds and along the margins of these vernal pools, and often is masked by *Eryngium* and *Deschampsia danthonioides.* Sometimes, though, this grass is noticeable on the somewhat barren portions of the pools. The species generally is not abundant, and is certainly not a conspicuous element of its habitat. One or two pools were found supporting many plants of the

species, while most pools had none, or, if a few, the plants went unnoticed among other vegetation. In one pool the grass was associated with a related annual, *Agrostis microphylla* var. *intermedia* Beetle, remarkably distinctive from the pale green and shining panicles of *A. tandilensis* by its reddish panicles, but also easily overlooked among the ubiquitous *Deschampsia danthonioides*.—Beecher Crampton, Agronomy Herbarium, University of California, Davis.

CALIFORNIA BOTANICAL SOCIETY
PUBLISHERS OF MADROÑO

REPORT OF THE TREASURER FOR 1956

Receipts:		
Balance on hand in commercial account, January 15, 1956	$ 464.15	
From memberships and subscriptions	2,369.35	
From sales of back numbers of *Madroño*	281.00	
Receipts from annual dinner	170.50	
Received as authors' share of publication costs	76.60	
Contributions to endowment fund	2.50	
Contributions to memorial fund	185.00	
Total receipts		$3,549.10
Disbursements:		
Credited to endowment fund from sales of back numbers of *Madroño*	$ 281.00	
Credited to endowment fund from contributions	2.50	
Credited to memorial fund	185.00	
Corresponding Secretary's expenses	62.15	
Cost of annual dinner	163.08	
Cancellation refunds	6.50	
Cost of printing, binding, and mailing *Madroño*, Volume 13, Numbers 5, 6, 7, and 8	2,008.57	
Total disbursements		$2,708.80
Balance on hand in commercial account, American Trust Co., Palo Alto, January 15, 1957		$ 840.30
Endowment and Memorial Fund:		
Palo Alto Mutual Savings and Loan Association, balance on hand January 15, 1957	$3,998.72	
Accrued interest	119.25	
From sales of back numbers of *Madroño*	281.00	
Contributions to memorial fund	185.00	
Contributions to endowment fund	2.50	
American Trust Company, savings account, balance January 15, 1957	$ 372.58	$4,586.47
Accrued interest	7.48	
		380.06
Total endowment		$4,966.53

Accounts audited and found correct:
Richard W. Holm, Auditor
June 6, 1957

Malcolm A. Nobs,
Treasurer for 1956

DOCUMENTED CHROMOSOME NUMBERS OF PLANTS

(See MADROÑO 9: 257–258. 1948.)

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
COMPOSITAE				
Aphanostephus arizonicus A. Gray	n = 4	R. C. Jackson, UNM[1]	*Jackson 2059*, UNM	Bernalillo County, New Mexico
**Engelmannia pinnatifida* Nutt.	n = 9	R. C. Jackson, UNM	*Jackson 2042*, UNM	Torrance County, New Mexico
Gaillardia pinnatifida Torr.	n = 17	R. C. Jackson, UNM	*Jackson 2033*, UNM	Bernalillo County, New Mexico
**Haplopappus spinulosus* ssp. *typicus* H. M. Hall	n = 4	R. C. Jackson, UNM	*Jackson 2032*, UNM	Torrance County, New Mexico
**Helianthus formosus* E. E. Watson	n = 51	R. C. Jackson, UNM	*Jackson 742*, IND	Marion County, Missouri
**Hymenoxys argentea* (Gray) K. F. Parker	n = 15	R. C. Jackson, UNM	*Jackson 2038*, UNM	Bernalillo County, New Mexico
**Melampodium leucanthum* Torr. & Gray	n = 10	R. C. Jackson, UNM	*Jackson 2082*, UNM	Bernalillo County, New Mexico
**Psilostrophe tagetina* (Nutt.) Greene	n = 16	R. C. Jackson, UNM	*Jackson 2049*, UNM	Torrance County, New Mexico
CRUCIFERAE				
Streptanthus amplexicaulis (Wats.) Jeps.	n = 14	A. R. Kruckeberg, WTU	*Kruckeberg 1553*, WTU	San Gabriel Mountains, Los Angeles County, California
**Streptanthus Howellii* Wats.	n = 14	A. R. Kruckeberg, WTU	*Kruckeberg 1881*, WTU	Siskiyou Mountains, Josephine County, Oregon

(continued on p. 112)

* Prepared slide available.

[1] Symbols for institutions are those listed by Lanjouw and Stafleu, Index Herbariorum, Part I. Second edition, 1954, Utrecht.

Species	Number	Counted by	Collection	Locality
Liliaceae				
**Fritillaria camtschatcensis* (L.) Ker-Gawl.	n = 12	R. Ornduff & A. R. Kruckeberg, WTU	*Kruckeberg & Ornduff 4013*, WTU	Stillaguamish River, Snohomish County, Washington
Portulacaceae				
**Lewisia Tweedyi* (Gray) Robins.	n = 46	A. R. Kruckeberg, WTU	*Kruckeberg 3320*, WTU	Wenatchee Mountains, Chelan County, Washington
Ranunculaceae				
**Delphinium bicolor* Nutt. forma *Helleri* (Rydb.) Ewan	n = 8	R. Ornduff, UC	*Hitchcock & Muhlick 20781*, WTU	About 20 miles east of Prineville on road to John Day, Crook County, Oregon
**Nuttallianum* Pritz. ex Walpers	n = 8	R. Ornduff, UC	*Hitchcock & Muhlick 20862*, WTU	About 2 miles east of Plains, Sanders County, Montana
**cyanoreios* Piper var. *cyanoreios*	n = 8	R. Ornduff, UC	*Hitchcock & Muhlick 20820*, WTU	About 18 miles south of Idaho City, Boise County, Idaho
			20835, WTU	About 21 miles west of Lowman, Boise County, Idaho
			20837, WTU	Two miles north of Cascade, Valley County, Idaho
**cyanoreios* Piper forma *multiplex* Ewan	n = 8	R. Ornduff, UC	*Hitchcock & Muhlick 20880*, WTU	About 10 miles northwest of Ellensburg, Kittitas County, Washington